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THE SPREAD OF VIRUS DISEASE IN CACAO

J. M. THRESH

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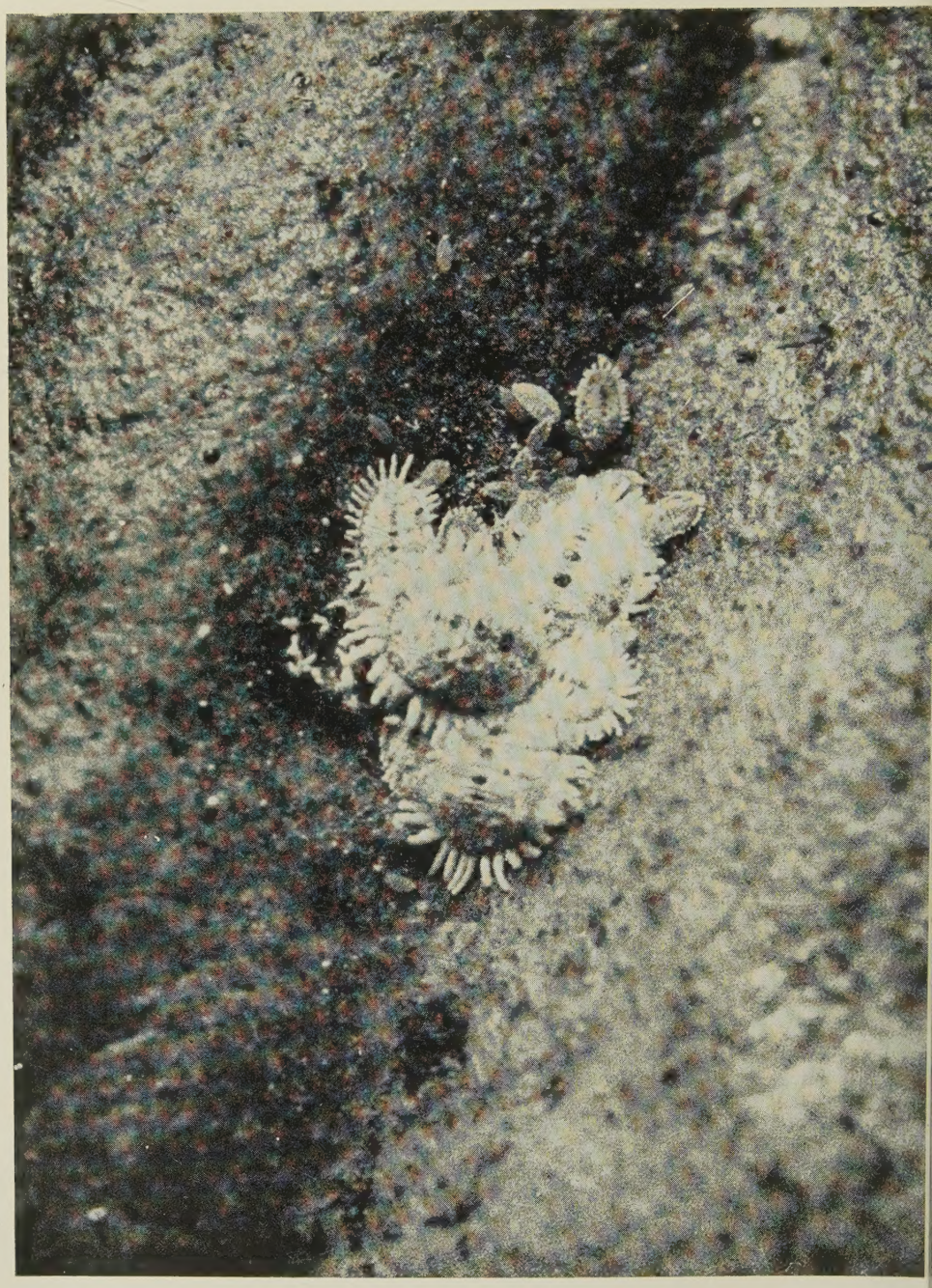

Pseudococcus njalensis Laing, the principal vector of cacao swollen shoot disease in Ghana; a colo
of nymphs and adults on the surface of a maturing pod.

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THE SPREAD OF VIRUS DISEASE IN CACAO*

	Page
INTRODUCTION	4
THE FORMATION OF NEW OUTBREAKS	5
The Spread of Virus from Wild Hosts	5
The Spread of Virus from Cacao	7
The Spread of Virus from Pods	8
The Spread of Virus from Planting Material	10
THE PATTERN OF SPREAD	10
THE RATE OF VIRUS SPREAD	14
FACTORS INFLUENCING THE SPREAD OF VIRUS	16
The Size, Composition, Distribution and Behaviour of the Mealybug Population	16
Seasonal Effects	18
Virus—Host—Vector Relations	19
The Age, Spacing and Condition of Tree	20
THE CONTROL OF VIRUS CONSIDERED IN RELATION TO SPREAD	21
Control by Eradication Measures	21
The Ancillary use of Insecticides	23
Replanting Devastated Areas	24
The Use of Resistant Varieties	24
Mild Strain Protection	25
SUGGESTIONS FOR FUTURE WORK	25
Mealybug Studies	26
Virus Studies	26
SUMMARY	27
REFERENCES	29
APPENDIX	33

* This review is based on publications which appeared by the end of 1957 and also refers to additional papers which were seen in manuscript.

INTRODUCTION

In 1938, Posnette (1940) showed that the swollen shoot condition of cacao in Ghana was caused by a virus. Subsequently, virus diseases of cacao were found in Nigeria (Murray, 1945), Ivory Coast (Alibert, 1946), Trinidad (Posnette, 1943a) and Ceylon (Peiris, 1953; Carter, 1956); and symptoms similar to those caused by virus infection have been noted in Venezuela (Posnette & Palma, 1944), Colombia (Ciferri, 1948) and Java (Thung, unpublished information).

A large number of virus isolates have been made from diseased cacao and the symptoms they cause have been followed on uniform seedlings grown under partially controlled conditions in glass houses. In this way many different isolates have been characterised by the symptoms they cause. Most of the West African isolates and some of those in Ceylon produce stem swellings and leaf symptoms of various types; some produce swellings as the only permanent symptom, whereas others, including ones from Trinidad, only cause leaf symptoms. This indicates that a large number of different strains of viruses attack cacao; a conclusion substantiated by the results of protection tests (Anon., 1948), host range investigations (Posnette, Robertson & Todd, 1950; Tinsley & Wharton, 1958) and vector studies (Posnette, 1950). Thresh & Tinsley (1958) have recently discussed these criteria for classifying the various West African isolates and suggest that they can be ascribed to three distinct viruses. Of these, the isolates of cacao necrosis virus have only been found in a few localities in a part of western Nigeria; their method of spread is unknown and they have not been experimentally transmitted by mealybugs (Posnette, 1950; Thresh, 1958b). Similarly the cacao mottle leaf virus is also restricted in distribution and appears primarily to infect the baobab, *Adansonia digitata* L. (Attafuah & Tinsley, 1958).

The present paper on the spread of cacao viruses therefore deals principally with the spread of the complex of strains causing cacao swollen shoot disease *per se* in West Africa. However, the spread of viruses in Trinidad is also discussed as these appear to be in the same virus group. The way in which new outbreaks can occur is described and an attempt made to assess the importance of the various sources of infection. The pattern and rate of virus spread is also discussed, together with factors likely to influence both the rate of spread and the efficiency of the various possible control measures.

THE FORMATION OF NEW OUTBREAKS

Experiments and experience suggest that the only form of natural spread is by the mealybug vectors, which pass from infected to healthy plants by walking or by wind currents. There is no evidence that the disease is seed or soil-borne, or transmitted between plants by contact, while the natural root grafts which may form between trees (Posnette, unpublished information) appear to be rare (McKelvie, unpublished information). Consequently outbreaks of swollen shoot disease are believed to be started by mealybugs reaching healthy trees from the various sources of infection, which in West Africa and Trinidad comprise:

(*a*) infected cacao trees;
(*b*) infected pods which are moved at harvesting;
(*c*) infected planting material.

Also, at least in West Africa, wild hosts are infected with cacao viruses. The formation of outbreaks by the movement of mealybugs is discussed in the following sections and an attempt is made to assess the relative importance of the different sources of infection.

The Spread of Virus from Wild Hosts

Posnette *et al.* (1950) and Tinsley & Wharton (1958) have investigated the host range of eight virus isolates from cacao in Nigeria and Ghana. They found that cacao viruses infect a number of species in each of the three families of the Tiliales, while more recently Dale & Attafuah (1957) showed that the host range extends into the related Malvaceae of the order Malvales. Many of the susceptible species are indigenous to West Africa and occur in cacao areas. Consequently they are potential hosts of cacao viruses and many attempts have been made to demonstrate natural infection, although various problems have been encountered in this work. For example infection cannot be recognised with certainty by a simple examination for symptoms and samples from suspected trees must be tested by infesting them with mealybugs and then transferring these to healthy cacao. It is not always easy to detect virus in hosts other than cacao, even when this method is used to test infected seedlings in the laboratory. Tests on material from the field are even less successful and it is difficult to obtain satisfactory samples from the larger trees, which may be 200 ft. or more in height. Nevertheless, in Ghana, virus occurs in *Cola chlamydantha* K. Schum., *Ceiba pentandra* Gaert., *Cola gigantea* var. *glabrescens* Brennan *et* Keay (Posnette *et al.*, 1950; Todd, 1951a) and in the baobab *Adansonia digitata* L. (Attafuah & Tinsley, 1958).

Cola chlamydantha

C. chlamydantha is a small understorey tree of the forest parts of the Western Province in Ghana and surveys show that virus can be transmitted from a high proportion of the naturally occurring trees, which are often infested with mealybugs of species occurring on cacao. Viruses from *C. chlamydantha* trees in several localities infected cacao seedlings and caused swellings and leaf symptoms indistinguishable from those caused by viruses from adjacent cacao.

This indicates that at least some of the outbreaks of virus in cacao have started by the spread of mealybugs from infected *C. chlamydantha* trees, or that these had been infected by spread from cacao. There is no conclusive evidence, but the discovery of infected trees in forest reserves some miles away from the nearest cacao and in unprotected forest which is only just being cleared for planting, is a strong indication that *C. chlamydantha* trees are naturally infected with viruses which have only begun to attack cacao since this crop was introduced into the area in the present century. Whether this hypothesis is correct or not, the large numbers of infected *C. chlamydantha* trees in and around the cacao farms of the Western Province in Ghana now provide an important reservoir of infection from which virus can spread to existing cacao and to cacao which is being planted in new areas and to replace trees which are being cut out in disease control operations.

Ceiba Pentandra

It has proved to be particularly difficult to transmit virus from *C. pentandra* trees to cacao, even from trees or seedlings which were known to be infected (Todd., 1951). Nevertheless, Posnette *et al.* (1950) transmitted virus from two of the fifty-two trees which were tested at Tafo and from a small plant collected near Offa Igbo in Nigeria. Virus has subsequently been obtained from other *C. pentandra* trees at Tafo, but there is no detailed information on the relationships between the viruses obtained in this way and those attacking cacao. Similarly, it is not known whether infection is restricted to areas where swollen shoot disease is to be found in cacao, or whether infected trees occur in areas where swollen shoot disease has not been reported. This makes it difficult to assess the importance of *C. pentandra* trees as hosts of cacao viruses. However, the low availability of virus to mealybugs feeding on infected trees and the relatively low density at which they occur in the cacao areas, indicate that *C. pentandra* trees are of little importance in areas where infection is already present in cacao. They may be more important in areas where viruses on cacao are limited in distribution, or in areas where infected trees have been completely eradicated.

Adansonia digitata

In Ghana naturally occurring baobabs are infected with viruses readily transmissible to cacao by mealybugs (Tinsley, 1955; Dale & Attafuah, 1957; Attafuah & Tinsley, 1958). Baobabs are commonly infested with mealybugs and are often found near villages in the cacao areas of Ghana and Nigeria, where they are clearly potential sources of infection. However, most of the infected trees have been found in the savannah country north and south of the forest areas in which cacao is grown. Moreover, the viruses which have been transmitted from baobab are of a type found only on cacao near Kpeve and Wusuta in Togoland and near Alaparun in Nigeria. Thus this wild host is probably not an important source of infection in the field.

Cola gigantea, etc.

One naturally occurring seedling of *C. gigantea* has been found to be infected with a cacao virus, but numerous attempts to transmit virus from mature trees have failed. Consequently, *C. gigantea* is probably of little importance as a field source of infection. Similarly, other plants known to be susceptible to cacao viruses have not been found infected in the field and they are probably unimportant now that infection is established in cacao, although they may have been of greater importance in the past.

Most of the above work was done in Ghana; but *C. chlamydantha* also occurs in Sierra Leone, Liberia, Ivory Coast and possibly in Nigeria, and baobabs occur at least in the savannah areas of these countries. Other possible hosts of cacao viruses also occur in the cacao areas of West Africa and elsewhere. It is therefore possible that the cacao in Ceylon and Trinidad became infected by the spread of virus from indigenous or introduced trees. Furthermore other viruses which are new to cacao may yet be found spreading from wild hosts in countries now thought to be free from infection.

The Spread of Virus from Cacao

Whatever the significance of alternative hosts in the past, most of the outbreaks now being found in cacao have undoubtedly started by the movement of mealybugs within the crop, virus having been allowed to spread in cacao with little or no check until quite recent times. Thus infected cacao trees are now the most extensive and potent sources of infection in most of the infected areas; also virus in infected trees is usually available to feeding mealybugs, which occur in substantial numbers, at least until infection is well advanced (Strickland, 1951b; Cornwell, 1956).

Swollen shoot disease was discovered in Ghana at Effiduase in the

New Juaben District in 1936 (Steven, 1936), although the disease was probably present in the nearby Nankese area as long ago as 1922 (Paine, 1945). Steven recognised the infectious nature of swollen shoot disease and as a control measure 81,000 trees were destroyed on 300 farms in 1936 and 1937. These measures were then discontinued until 1945. By that time swollen shoot disease was widespread in the Eastern Province of Ghana and was also present in Ashanti, Western Province and Togoland. Control of the disease over such a large area of difficult country has presented many problems and by the end of 1956, 63 million infected trees had been cut out (Hammond, 1957). Nevertheless, virus has been eradicated from only 2 per cent. of the treated farms and nearly 1 million infected trees are still being removed each month.

Swollen shoot disease was first discovered in Nigeria in 1944, but was then so widespread that it must have been present for many years. Eradication measures are now abandoned in two large areas of cacao, where several million infected trees are known to occur. Virus, allowed to spread there unchecked, is spreading to the healthy cacao outside. An increasing number of new outbreaks are being found, even in areas where control measures are applied and it is increasingly difficult to keep these free or relatively free from infection (Lister & Thresh, 1957; Thresh, 1958a).

Elsewhere in West Africa swollen shoot disease is established in some of the most important cacao growing areas in Ivory Coast and is becoming more widespread, as only limited control measures have been adopted (Renaud, 1957). Outside West Africa, cacao virus diseases are not so important, but early observations in Trinidad showed that infected trees occurred in some of the most important cacao areas at the Western end of the Northern Range (Baker & Dale, 1947a). Similarly viruses have been present at a number of plantations in Ceylon for some years (Orellana & Peiris, 1957). There is no recent information on the distribution of infection in either country, but in the absence of any general control measures it may be assumed that the early outbreaks have spread and also increased in number.

The Spread of Virus from Pods

Harvested ripe pods are usually collected together in a pile, often at the same site each year, usually in a shady part of the cacao farm and often under particularly vigorous trees with a dense canopy. The pods are then broken, the beans removed and the husks left to rot. Thus mealybugs are carried to the piles, although the number distributed in this way is not known. In both Ghana and in Nigeria,

however, a substantial proportion of the mealybugs which occur on mature trees are present on the pods (Strickland, 1951a; Donald, unpublished information), and mealybugs feeding on pods taken from trees infected with cacao swollen shoot disease can transmit virus (Dale, 1956). In this way virus may be carried to a healthy part of a farm during harvesting, or from the wilting and decomposing pods discarded after the beans have been removed. The proportion of outbreaks started in this way is not known and there have been no detailed observations on the incidence of swollen shoot disease in relation to the sites where pods are piled. Nevertheless, Posnette (unpublished information) noted that many of the earliest outbreaks of swollen shoot disease were found in such localities in the New Juaben area of Ghana. This indicates the probable importance of harvesting operations in the spread of virus, although in the small West African farms spread in this way is likely to be over relatively short distances.

The movement of pods over long distances for seed material is probably more important; such movement is considerable both in Ghana and in Nigeria, by private individuals and also on a large scale by the Departments of Agriculture. Intact pots are also exchanged between countries and large consignments have recently been sent from Ghana to Nigeria, the Cameroons and elsewhere. Some of these pods are from areas where infection is widespread, and from Amazon types known to tolerate virus infection without showing obvious symptoms (Posnette & Todd, 1951; Dale, 1957). Thus there is a risk of virus spread over considerable distances, which may explain the appearance of outbreaks in areas remote from the nearest sources of infection. For example the viruses from infected cacao near Kongodia in Ivory Coast and near Konongo in Ashanti are virtually indistinguishable from those otherwise apparently restricted to the New Juaben area of Ghana (Tinsley, 1955), and may have been spread in this way.

Thus movement of pods between growing areas needs rigid control. Pods should be taken only from trees which are inspected for swollen shoot disease at regular and frequent intervals. Moreover the pods must be treated to kill any mealybugs on them before distribution, and the husks destroyed immediately the beans are removed. There is then little likelihood of virus spreading from them, although dipping pods in insecticide is not always effective against mealybugs, as these are difficult to wet, even when they are exposed. Moreover they are commonly protected by carton nests or in cracks or the mines and holes caused by other insects. Further work is needed on the best method of sterilising these damaged pods.

The Spread of Virus from Planting Material

In West Africa most of the farms have been established from seed, which does not carry swollen shoot virus (Posnette, 1947). However, in Trinidad large numbers of rooted cuttings are distributed to farmers. These, if taken from infected trees, could introduce virus into new areas and there is evidence of outbreaks following the movement of infected material in Trinidad (Baker & Dale, 1947b) and Ceylon (Orellana & Peiris, 1957). Consequently great care is necessary to multiply only healthy material and propagating stations should if possible be in areas remote from the nearest sources of infection, where the trees are regularly examined for virus symptoms. With clones which tolerate infection it may also be necessary to test them at regular intervals by grafting to susceptible indicator stocks.

Such precautions will be needed in West Africa, where increasing numbers of cuttings are being planted for the large-scale production of improved seed. Also cuttings of particularly valuable clones may become available to farmers, as in Trinidad. Many of the clones being multiplied in West Africa have been selected and developed at Tafo, where swollen shoot disease occurs. They include types which tolerate infection and the propagation and distribution of selected clones will have to be rigidly controlled in future.

The quarantine arrangements for moving rooted cuttings between countries pose a number of problems. Only a limited amount of growth may occur during the conventional quarantine period, with little likelihood of symptoms being found, particularly on the usual fan cuttings, which show relatively inconspicuous symptoms when they are infected. This is a particular difficulty when dealing with tolerant clones and there is little information on the time taken for virus to appear in such material. It is suggested therefore that breeding material should pass between countries as bud-wood, which can be propagated on susceptible indicator stocks. If this is done before the bud-wood is dispatched and also in the receiving country, then the chances of virus spread will be far less than with the present system of transporting rooted cuttings.

THE PATTERN OF SPREAD

The incidence and distribution of outbreaks of swollen shoot disease is influenced by the nature of the sources of infection. New outbreaks are formed continuously in areas of widespread infection, but the pattern of spread is usually so complex that the precise origin of most outbreaks is obscure. By comparison, new outbreaks can usually be related to previous centres of infection in areas where outbreaks are

scattered, but not widespread. Moreover infection in cacao can sometimes be traced to infected alternative hosts, as with numerous scattered outbreaks in the Western Province of Ghana, where infected *C. chlamydantha* trees are within and alongside infected farms. However near Ife and Ilesha in Nigeria, isolated outbreaks have been found many miles away from the nearest known source of infection, possibly as a result of the transport of mealybugs on pods or by air currents.

Observations on the spread of individual outbreaks were started before mealybugs were found to be the usual vector and showed that most of the new infections occurred close to trees already showing symptoms (Posnette, 1943b). Spread was not always continuous and some of the newly infected trees were not in immediate contact with obviously infected ones and subsidiary outbreaks occasionally arose at some distance from the original source. This has been repeatedly confirmed elsewhere in Ghana, Nigeria and Trinidad. Thus Dale (1953) followed the spread of virus in regularly planted plots of clonal cacao in Trinidad and his diagrams show clearly that most of the new infections developed amongst trees in contact with those showing symptoms. The same occurs in irregularly planted peasant farms in Nigeria (Thresh, unpublished information); at one plot near Ibadan 74.8 per cent. of the new infections appearing between 1953 and 1957 occurred within 5 yds. of trees already showing symptoms, 15.5 per cent. occurred between 5 and 10 yds. and 4.1 per cent. occurred between 10 and 15 yds. These experiments probably underestimate the proportion of new infections occurring in contact with infected trees, a substantial proportion of which may be symptomless at any one time, while other recently infected trees may still be in the latent phase (Thresh, 1958a). At least some of these trees may act as sources of virus to feeding mealybugs (Thresh, 1958b). Indeed, symptomless infected trees are particularly dangerous, as they are likely to support a higher mealybug population than trees in a more acute stage of infection and mealybugs may move away as symptoms develop (Cornwell, 1956). Moreover, recently infected trees are usually more vigorous than severely affected ones and are more likely to be in contact with their neighbours.

Coppicing experiments in Nigeria (Lister & Thresh, 1957; Thresh, 1958a; 1958c) gave the most complete data on the distribution of new infections. Obviously infected trees at each of forty-eight outbreaks were uprooted and the adjacent apparently healthy trees were coppiced to a distance of 30 yds. The new growth from the coppiced stumps was inspected regularly and the incidence and distribution of infections discovered in this way were recorded in relation to the trees uprooted at the outset. A curvilinear relationship, similar to

that described by Gregory & Read (1949) for the spread of other insect-borne plant virus diseases, was obtained between the percentage number of infected stumps and their distance from the site of the nearest uprooted infection. The general equation being:

$$\text{Log } I = a + b\,x$$

Where I represents the percentage number of infected stumps at distance x. The constant a expresses the height of the regression line and increases with size of outbreak. The constant b expresses the slope of the regression line, is always negative and is approximately the same for outbreaks of all sizes. It should be noted that the equation expresses latent infection, largely due to spread immediately before this was checked by coppicing. Extrapolation of the regression line suggests that swollen shoot disease spreads in considerable amount only over limited distances. Around the larger outbreaks the intensity of latent and missed infection in trees 30 yds. from the uprooted trees was approximately 1.23×10^{-1} and intensities of 3.0×10^{-4} and 9.0×10^{-7} are estimated for trees 60 and 90 yds. distant. The low probability of infections at these distances means that they eventually appear as 'subsidiary' outbreaks, surrounded by healthy trees.

In West Africa the short distance movement of virus between trees is known as radial spread (although this is rarely uniform in all directions and most outbreaks have an irregular outline) and over greater distances as discontinuous or jump spread. The accompanying diagrams, Appendix II, indicate the pattern of spread when virus is unchecked for a number of years in a continuous stand of cacao. They are based on observations and coppicing experiments in Nigeria and on actual sketch maps prepared by the Nigerian Department of Agriculture. The horizons of infection beyond which the intensity of latent infection is less than 5 per cent. occur at a greater distance from the outbreaks as these increase in size. Moreover, the probability of subsidiary outbreaks occurring around the centres of infection increases as these increase in size and decreases with increasing distance from them. The subsidiary 'satellite' outbreaks probably occur by occasional jump spread of virus from the main centres of infection. This assumption gives the most plausible explanation of the occurence of satellite outbreaks and appears to be justified in most instances, particularly in areas of scattered infection where outbreaks are discontinuous and separated by considerable distances. However, some outbreaks may be started by mealybugs coming in from an outside source of infection, either cacao or an infected wild host.

Most of the work on vector behaviour has been carried out at Tafo where the mealybugs are almost all *Pseudococcus njalensis* Laing (Strickland, 1951b), but how far these observations apply to other species,

which may be important or even dominant on other areas is conjectural. The work at Tafo has shown that mealybugs may spread

(*a*) by walking through the canopy or along the ground (Strickland, 1951a; Cornwell, 1956, 1958);

(*b*) by wind currents (Strickland, 1950; Cornwell, 1955, 1957b);

(*c*) when they are carried by ants (Cornwell, 1957b).

Passage from tree to tree along the ground appears to be unimportant (Strickland, 1951a; Cornwell, 1956), and although adult mealybugs have occasionally been seen in the mouth of ants, spread in this way is probably rare (Cornwell, 1957b). Consequently, movement of mealybugs through the canopy and by wind currents is deemed to be responsible for most of the spread of swollen shoot disease. Frequent movement through the canopy appears to take place only over short distances (Cornwell, 1958) and this probably accounts for most of the spread from infected trees to adjacent healthy 'contacts'. Mealybugs carried by wind probably account for some spread to adjacent trees and for most of the spread over greater distances.

There is little information on the relative importance of the two types of spread, or on the proportion of mealybugs which move from infected trees, but at Tafo 90 per cent. of the mobile mealybugs were first instar nymphs (Cornwell, 1957b). These are efficient vectors under experimental conditions (Posnette & Strickland, 1948; Lister, 1953; Dale, 1958) and presumably in the field, but at least some may migrate before they have become infective. These points require further investigation; meanwhile, evidence suggests that the spread of virus by the aerial movement of mealybugs is probably infrequent and this conclusion is supported by the steep gradients of infection found around outbreaks and by the limited rate and extent at which these spread. Thus plots in which control measures are practised can be maintained free or relatively free from infection, even where they adjoin abandoned areas where infection is widespread (Benstead, 1953). Moreover, only a limited amount of spread has been recorded in the cacao around the two large and heavily infected areas in Nigeria where control measures have been abandoned and virus has been spreading without check for some years (Lister & Thresh, 1957; Thresh, 1958a). Similarly in Ghana, most of the cacao appears free from infection, even though virus has been present for many years and control measures were only started in relatively recent times. The limited amount and extent to which virus has spread in West Africa over a period of years should be compared with the spread of viruses of annual crops such as sugar beet yellows, which may affect virtually the whole crop in the British Isles in a few months. Clearly swollen shoot may be regarded as a 'crowd' disease, of the type

discussed by Van der Plank (1948) and defined by him as one which does not spread far in considerable amount.

THE RATE OF VIRUS SPREAD

All available data on the spread of swollen shoot disease are on the appearance of trees with symptoms, which gives only an approximate indication of the rate of spread, as the detection of infected trees is difficult and the latent period of infection may be long and variable and probably depends upon season and the condition of the trees at the time they are infected (Thresh, 1958b). Most of the observations have been on natural outbreaks in plantations or peasant cacao in Ghana, Nigeria and Trinidad. Only in Ghana has it been possible to inoculate healthy trees in the field and carry out a few statistically designed experiments on spread. Consequently the experimental data are very varied, being for different seasons, countries, and viruses; and in cacao which was not uniform in age, spacing, type or condition.

The observations on virus spread have been further limited by the size of the plots, which soon became completely infected, as in the so-called 'rate of destruction experiment' at Tafo (Benstead, 1953). Between 1945 and 1951 the virulent New Juaben virus was allowed to spread unchecked in 8¼ acres of irregularly planted cacao, where the tree population at the outset was 4,636. Symptoms were found on 1,450 trees in 1945, the yearly number of new infections reaching a maximum in 1948, when 80 per cent. of the trees were infected. Fewer new infections were seen in subsequent years and the experiment was abandoned in 1951 with 92 per cent. of the trees showing symptoms (Appendis III, Table 1). In Trinidad (Dale, 1953) the spread of virus into the 576 clonal trees of the experimental area CRBI at River Estate showed the same trend (Appendix III, Table 3), the number of new infections annually increasing from 46 in 1946 to a maximum of 102 in 1947 and then progressively declining to 20 in 1951. This tendency for the number of infected trees on a plot to follow a sigmoid trend with respect to time has been observed elsewhere in the Western Province of Ghana (Posnette & Todd, unpublished information) and also in Nigeria (Lister & Thresh, unpublished information) (Appendix III, Table 2). Indeed it is a general feature of spread within a limited population. In Nigeria the number of new infections annually increased as the number of apparently healthy trees contacting obviously infected ones increased. Then, when approximately half the trees on the plots were infected, the number of contacts and new infections decreased; a further indication of the importance of spread between adjacent trees.

The tendency to underestimate the spread of virus when plots are

of limited size and become heavily infected, may be partially overcome using the multiple infection transformation (Gregory, 1948). In this way a more realistic estimate of spread is obtained until most of the trees are infected (Appendix III). However, the transformed values for the percentage number of infected trees still follow a sigmoid trend with time. This relationship differs from that expected for uninterrupted spread in an unlimited area of cacao. In these circumstances the number of healthy trees in contact with infected ones increases progressively, and an increasing number of new infections may be expected each year.

The variation between observation plots makes it difficult to compare the apparent rate of spread at different sites. However, the data show that the annual number of new infections appearing around an outbreak is not directly proportional to the number of infected trees present at the beginning of the period and the rate of virus spread varies according to outbreak size. The number of infections appearing each year around small outbreaks equals or exceeds the number of trees infected at the beginning of the period. By comparison, the number of new infections appearing each year around large outbreaks is only a proportion of the trees known to be infected in the previous year. This is illustrated by the data for spread in Trinidad (Appendix, Table 3).

The data from the Nigerian coppicing experiments also suggest that rate of spread varies with size of outbreak. The smallest outbreaks contained an average of 3.9 infected trees at the time of coppicing and an average of 3.2 infected stumps were found around each outbreak, a ratio of 1.0 : 0.82. The largest outbreaks contained an average of 142 obviously infected trees and an average of fifty-one infected stumps were found around each outbreak, a ratio of 1.0 : 0.36. Most of the infected stumps were recent infections still symptomless when coppiced and their incidence in relation to the number of obviously infected trees is a further indication that large outbreaks are spreading less rapidly than small ones, if the rate of spread is taken as the number of new infections expressed as a percentage of the number of existing ones.

This tendency is to be expected as most of the infected trees in small outbreaks are in contact with healthy ones and virus may be spread by mealybugs moving through the canopy or on wind currents. By comparison, in large outbreaks relatively few viruliferous mealybugs can reach healthy trees by movement through the canopy and the relatively infrequent wind dispersal is probably more important. The spread of virus from infected trees within outbreaks is further limited by the tendency of their mealybug populations to decline as the trees deteriorate (Strickland, 1951b; Cornwell, 1956). Clearly

spread is usually from infected trees on the perimeter of an outbreak. These may be showing symptoms or in a latent phase, but they are likely to support relatively high mealybug populations, even though virus is not always readily available. The importance of symptomless trees and trees which have only recently produced symptoms is indicated by the limited success of eradication measures in Ghana. Infected trees are destroyed when found during monthly inspections of diseased farms, yet the larger outbreaks are not readily controlled in this way and virus often continues to spread after treatment (Posnette, 1943b; Hanna & Heatherington, 1957; Hammond, 1957; Thresh, 1958a, 1958d).

The data from some observation plots enable comparisons to be made of the rate of spread around outbreaks originally containing the same number of infected trees. For example, at Offa Igbo, the number of infected trees increased from 50 to 100 in four months and from 50 to 200 in sixteen. At the nearby Koroboto plot comparable increases occurred in thirteen and twenty-two months respectively, evidence that rate of spread varies between sites. Some of the reasons for these differences are discussed in the following sections.

FACTORS INFLUENCING THE SPREAD OF VIRUS

Experiments and observations on the interactions between virus, host and vector indicate a number of factors which are likely to influence the rate of virus spread and these factors are discussed under the following sub-headings. However, the available results on spread are so imprecise that there is no detailed information of the significance of the various factors.

The Size, Composition, Distribution and Behaviour of the Mealybug Population

Studies on populations of mealybugs in Ghana, Nigeria, Trinidad and Ceylon show that they occur on all parts of the cacao tree, including roots, flowers, cherelles, pods, bark, twigs and leaves. The numbers are usually low and at Tafo in Ghana, Strickland (1951b) found an average of 65.7 mealybugs per tree, although there were considerable differences between populations on trees in the same and in different areas. At six adjacent sites 396 trees had no mealybugs, whereas sixteen supported more than 800 mealybugs per tree. Virtually all the mealybugs were of the efficient vector *P. njalensis* and these differences partly account for the irregular spread of virus.

In Nigeria, different species may be dominant in certain areas or

seasons (Donald, 1954, 1955, 1957) and five vector species are present in Trinidad; the commonest one being *Planococcus citri* (Risso) (Kirkpatrick, 1953). Not all the mealybug species are able to transmit cacao swollen shoot virus and some species may transmit certain isolates, but not others (Posnette, 1950). Moreover the different species probably vary in the efficiency with which they transmit a particular isolate. Consequently virus spread depends on the mealybug population and also on the species present.

At Tafo 75.5 per cent. of the mealybugs were feeding on fan shoots in the canopy (Strickland, 1951a), while approximately 81 per cent. of the mealybugs in Nigeria were on the upper parts of the trees (Donald, 1955). Thus most of the mealybugs on mature trees in a continuous stand of cacao can move on to adjacent trees by walking a short distance through the canopy. The chances of them doing so depend upon the spacing and condition of the trees and other factors discussed below.

Adults of *P. njalensis* in Ghana are sedentary and rarely move from their feeding sites, but the immature forms and particularly the first instar nymphs are quite active (Cornwell, 1958). However the percentage of *P. njalensis* which are mobile and the extent of movement between trees is not known. There is even less information on the behaviour of other vectors, but the indications are that some of them may be more active than *P. njalensis*. Strickland (1951a) observed that *P. citri*, *P. longispinus*, *P. concavocerarii* and *F. virgata* have longer legs than *P. njalensis*. Unlike *P. njalensis* these species are not usually attended by ants and probably rely on their own powers of locomotion to a large extent. A further indication that nymphs of *P. njalensis* are less active than those of other species is that the nymph to adult ratio for individual colonies is usually high, whereas the nymphs of other species often migrate and the ratio is comparatively low (Donald, unpublished information). The limited tendency for nymphs of *P. njalensis* to migrate may also explain the observation that relatively few mealybugs of this species were found on seedlings some distance away from cacao at Tafo (Cornwell, 1955). However, it may be that nymphs of *P. njalensis* are carried away by wind currents as frequently as those of other species, but that they fail to establish themselves on exposed seedlings, particularly if suitable ants are absent.

Two species of mealybug *P. concavocerarii* and *F. virgata* occur rather frequently on flowers and cherelles but are so uncommon on stem tissues that they are probably unimportant vectors in the canopy. Nevertheless the immature forms are carried into the air by wind currents and probably contribute to discontinuous spread, particularly as the nymphs of *F. virgata* develop two fine anal wax filaments which tend to support them in the air (Strickland, 1951a).

Seasonal Effects

Cornwell (1958) established that *P. njalensis* shows a periodic diurnal activity and the number of mealybugs taken on bait twigs placed in the canopy of infested cacao trees increased to a maximum at about 15.00 hours and was positively related to temperature. It might be expected therefore that movement between trees in West Africa is at a maximum at the hot equinoxial periods and at a minimum during the dry season and particularly during the cool cloudy conditions of July and August. The possibility that mealybugs are more active at certain periods of the year suggests that virus spread also varies with season; particularly as Cornwell (1957a) showed that the mealybug populations at Tafo varied with season and were at a maximum on infested trees in October and November, at a peak period of activity.

Recent experiments in Nigeria provide further evidence that peak periods of spread occur in West Africa and virus is more readily available to mealybugs feeding on the young stem tissues of recent flushes, than to mealybugs feeding on hardened tissues (Thresh, unpublished information). Thus at any particular population level mealybugs feeding on infected trees which are flushing vigorously are more likely to acquire virus than mealybugs on trees which are not making new growth. The flushing of trees in Trinidad (Humphries, 1944) and Ghana (Greenwood & Posnette, 1949) is positively correlated with temperature and the seasonal variation in virus availability and the tendency for mealybugs to be most numerous and active at the hotter periods of the year may well cause peaks of spread at these times.

The validity of this hypothesis is not easily tested, because observations on spread depend on symptom expression and the latent period is variable. Nevertheless, in Ghana and in Nigeria more new infections are found in October, November, March and April than at other times of the year. Although symptoms are most easily detected at these active periods of growth, the effect may be partly due to peak periods of spread occurring some months previously.

Under field conditions it is rarely possible to detect new outbreaks until they have spread for some years (Thresh, 1958a), and it is difficult to estimate even the approximate dates on which outbreaks were started. However, trapping experiments carried out by Strickland (1950) over twelve consecutive months at various sites in Ghana showed that most of the dispersal of mealybugs by wind currents took place during the dry months, suggesting that most new outbreaks of virus are started at these periods.

Virus-Host-Vector Relations

Mealybugs moving from infected trees can transmit virus only if they contain an infective dose which persists until they have fed for an adequate period on healthy trees. Thus spread partly depends upon the feeding behaviour of mealybugs before and after their migration and also upon factors influencing virus availability. These have been investigated in Ghana and Nigeria and the efficiency with which mealybugs transmitted virus from infected trees and seedlings varied with the virus, the stage of infection and the type of tissue which was tested. The availability of virus was closely associated with the severity and extent of the symptoms on the tested material and young shoots were a more satisfactory source than older tissues or pods (Posnette & Strickland, 1948; Posnette & Robertson, 1950; Posnette, 1950; Thresh, 1958b).

That different viruses may spread at different rates was shown by Crowdy & Posnette (1947) at Tafo and Posnette & Todd (unpublished information) in the Western Province of Ghana. At Tafo three viruses were introduced into experimental plots in 1942 and the virulent New Juaben virus spread more rapidly into control and border plots than viruses from Bisa and Kpeve. This difference probably depends upon the relative availability of the viruses and on the rapidity with which they multiply and become systemic; a conclusion supported by the Western Province results, where the virus which spread most rapidly was also the easiest to transmit in the laboratory.

There is little information on factors affecting susceptibility but certain varieties resist infection and may show field immunity (Posnette & Todd, 1951; Dale, 1956). Moreover mealybugs reaching healthy trees are more likely to settle, feed and infect their new host if satisfactory feeding sites are available and trees in an active period of growth are probably more susceptible than dormant ones.

Work in Ghana, Nigeria and Trinidad on virus-vector relations is summarised and discussed by Martini (1958). The probability of mealybugs transmitting virus increases with the number of vectors used and with the length of time they spend on source plants and test plants, up to optimum periods of several hours and fifty minutes, respectively. Virus persists less than three hours in feeding mealybugs, but starved ones transmit virus up to thirty-six hours or more after the infection feed. Thus virus can persist sufficiently long in migrating mealybugs to allow spread over considerable distances. However the limited persistence of virus in feeding mealybugs suggests a method of reducing spread by interplanting cacao with other crops or using barriers of edible cola or coffee. These are not susceptible to cacao viruses and mealybugs reaching them would quickly lose any virus they contain. These possibilities are discussed by Cornwell (1958)

and warrant further investigation, particularly where extensive replanting is done in areas where infection is widespread.

The Age, Spacing and Condition of Tree

When a cacao plantation is established the mealybug population starts at a very low level and builds up over the years, as colonisers settle and multiply. The rate of build-up has not been followed, but at Tafo Strickland (1951b) obtained a significant and positive correlation between girth and the percentage number of trees infested and found that large trees supported higher mealybug populations than small ones. Girth is an indication of age and these observations show that the incidence of mealybugs and the populations which occur both increase with the age of the tree. Thus the spread of virus outbreaks probably varies according to the age of the infected plantation, particularly as mealybugs can move more readily between trees as these increase in size and form a continuous canopy. In young plantations there is little chance of trees becoming infected by intercepting mealybugs blown from an outside source of infection and outbreaks which do occur spread slowly (Benstead, 1951, 1953). By contrast virus spreads more rapidly in mature plantations, as the trees are usually touching their immediate neighbours and spread may occur by movement through the canopy and by wind dispersal.

Contact between the branches of adjacent trees increases with time at a rate dependent upon the spacing and condition of the trees. Thus virus spreads most rapidly in closely spaced plots where the trees are making rapid growth. There have been no detailed experiments on spread in relation to tree density, but the importance of the effect is indicated by observations on spacing trials in Ghana (Cornwell, 1958) and Nigeria (Thresh, unpublished information). In Nigeria each of the twenty-eight eleven-year-old trees examined in plots at a uniform spacing of 5×5 ft. was in contact with an average of 6.2 other trees. Trees at 10×10 ft. and 15×15 ft. were each in contact with an average of 3.5 and 0.6 trees respectively. At the closest spacing the trees formed a continuous interlocking canopy and each tree was usually in intimate contact with most of its immediate neighbours and some other trees. By comparison the trees at the widest spacing were not usually in contact.

Cacao in West Africa is commonly attacked by capsids, which damage pods and branches and they predispose trees to attack by fungi causing dieback (Crowdy, 1947) and accentuate the decline of trees infected with virus. Capsids also influence virus spread, as severely damaged trees are rarely in contact with their neighbours and often make such poor growth that symptoms are difficult to

detect. However increased wind movement within severely damaged farms is likely to increase the relative importance of discontinuous spread, particularly as severely capsid damaged trees tend to support relatively high populations of mealybugs (Strickland, 1951b). This may be due to the greater number of breeding sites in the cankers and lesions of damaged trees, or to the relatively high populations of the Crematogasterine ants which are closely associated with some mealybugs and sometimes nest in dead twigs and branches (Hanna, Judenko & Heatherington, 1956).

THE CONTROL OF VIRUS CONSIDERED IN RELATION TO SPREAD

Control by Eradication Measures

The success of eradication measures in controlling a virus disease largely depends on the rate of virus spread. If this is rapid or if infection is difficult to detect, many recently infected plants are left behind each time the crop is inspected and rogued. Virus may spread from these missed infections and eradication measures are likely to be unsuccessful and uneconomic. However, if virus spreads slowly and is easily detected, removing the plants found with symptoms eliminates or greatly reduces the available sources of infection within the crop and spread can be effectively controlled, while virus may even be eliminated from whole areas.

The effectiveness of eradication measures in controlling swollen shoot disease was first demonstrated at Tafo (Posnette, 1943b) and is a further indication that the disease spreads slowly. Outbreaks of less than six obviously infected trees were sometimes eradicated merely by removing the trees found with symptoms. Larger ones were not eradicated so easily and latent or missed infections were left behind at the time of the initial treatment, although the outbreaks were usually controlled by repeating the inspection and roguing on subsequent occasions. It is time-consuming and inconvenient for the survey parties to keep on returning to the standing trees around treated outbreaks and this method of control is fundamentally inefficient as virus may spread between the initial treatment and subsequent detection of the missed trees. An alternative and more effective eradication method is to make the treatment more drastic and remove the trees found with symptoms and also the apparently healthy trees which were in contact with them.

These observations have been repeatedly confirmed elsewhere in Ghana (Anon., 1945) and in Nigeria (Thresh, 1958a). In the Nigerian experiments, removing the trees found with symptoms would

have controlled eighteen of the thirty-two outbreaks which contained less than six obviously infected trees, but only one of the forty-eight larger outbreaks. The same series of experiments also showed the value of removing the apparently healthy trees in contact with infected ones. Using these methods twelve of the sixteen outbreaks which contained less than six obviously infected trees would have been controlled and sixteen of the forty-six larger outbreaks. Thus small outbreaks are relatively easy to control and cutting out treatments should vary according to the size of outbreak. The Nigerian coppicing experiments have shown that the intensity of latent and missed infections is sufficient to justify recommending the eradication of apparently healthy trees to distances of 5, 10 and 15 yds. around outbreaks of 1–5, 5–50 and 50–200 infected trees respectively. Some outlying infections and subsidiary outbreaks will occur outside these distances and will eventually be found in the standing trees around the treated areas. However this is so unlikely that there is no justification for a more drastic initial treatment and it is suggested that outbreaks should be treated according to the number of infected trees found. The remaining standing trees in the area should then be kept under regular re-inspection and re-treated when necessary.

Similar recommendations probably apply to the treatment of outbreaks in Ghana. In both Ghana and Nigeria large sums of money are being spent on eradication measures which were introduced in attempts to reduce the extent of the heavily infected areas and safeguard new plantings. At the outset only the obviously infected trees were destroyed, but many of the treated outbreaks were large, with the result that the eradication measures were not immediately successful. Indeed the lack of success in Nigeria made it necessary to abandon control measures in first one and then a second major cacao area and efforts are now concentrated on maintaining the remaining cacao areas relatively free from infection (Lister & Thresh, 1957).

In Ghana only a limited number of new outbreaks are now being found in Ashanti, Trans-Volta & Togoland, the Nkawkaw Division of Eastern Region and the Eastern and Central Sections of the Western Provinces. Swollen shoot disease is being controlled in these areas, but many infected trees remain to be destroyed elsewhere in the Eastern and Western Regions. When the initial cutting out treatments have been carried out in all the infected areas, the remaining cacao can probably be maintained relatively free from infection without difficulty. This is indicated by experience at Tafo, where eradication measures have been practised on the 65 acres of 'Old Station' cacao since 1941 and on the 'Square Mile' since 1945 (Benstead, 1953). New outbreaks are being found continuously, but only 1–2 per cent. of the trees are cut out each year and control

measures have been successful, even though swollen shoot disease was until recently widespread in the adjacent cacao.

The Ancillary Use of Insecticides

The eradication measures used at present might be greatly increased in efficiency if insecticides could be used to control the mealybugs until all the missed infections have been found and destroyed during the re-inspections. If this could be achieved it might be possible to recommend the removal of contacts on a less drastic scale than at present.

Unfortunately, mealybugs are not easy to kill by contact insecticides, due to their cryptic habit, the protective wax covering on most species and their frequent occurrence under carton tents built by ants. However the systemic insecticide dimefox has given a satisfactory kill of mealybugs on trees treated by soil application or by trunk implantation (Hanna, Judenko & Heatherington, 1955) and has also given interesting results in a detailed field trial in which attempts were made to check virus spread (Hanna & Heatherington, 1957). This single and costly experiment was inadequately controlled, but applications of dimefox combined with eradication measures were claimed to be more effective than eradication measures alone in controlling swollen shoot disease and there was some evidence that spread was largely if not entirely arrested after the initial cutting out treatment had been carried out. The results of the Ghana experiments with dimefox justify more extensive work on the possibilities of systemic insecticides and work is proceeding at WACRI and in Costa Rica (Casida & Bowman, 1957). Some of the materials which are being tested are now widely used on certain crops and are much less toxic to mammals than dimefox.

An alternative possibility is to control the ants which tend mealybugs. Early experiments with D.D.T. were not encouraging (Hanna, Judenko & Heatherington, 1956), but subsequent experiments with dieldrin have given more promising results. This material, applied to the accessible parts of cacao and forest trees, caused a striking decrease in ant population, which was accompanied by a decline in the number of mealybugs (Taylor, 1957). Populations of ants and mealybugs remained at a relatively low level after treatment, depending upon the size of the area which had been sprayed (Entwistle, 1958). The relatively slow rate at which the larger areas became reinfested is a further indication of the limited extent to which mealybugs move or are carried over considerable distances. The preliminary results also justify the more extensive trials which are now being made to investigate the effect of dieldrin on the efficiency of routine eradication control measures.

Replanting Devastated Areas

To maintain yields in areas devastated by swollen shoot disease or by routine eradication control measures, it is necessary to establish new plantings. This is not difficult wherever the soils and climate are suitable; but virus may spread into the new plantings according to their proximity to remaining sources of infection. For example, infection readily spreads into the numerous small plots of farmers' cacao which are being established in the two areas of mass infection in Nigeria (Thresh, 1958a), where new plantings are often near or alongside infected trees. Similarly in Ghana heavily infected areas have remained untreated until recent years and in the 'resumed' areas almost half the sixteen million infected cut out trees were recently planted and were not bearing (Hammond, 1957). Infection is often scattered throughout the young cacao and may sometimes be related to the distribution of infected mature trees which survived from the original stand.

The extensive infection of young cacao in parts of Ghana and Nigeria is largely due to the unrestricted planting of small plots, without any attempt to remove the immediate and obvious sources of infection. If this is done and the new plantings are thoroughly inspected for swollen shoot disease at regular intervals, at least some areas can be satisfactorily brought into bearing without serious losses. At Tafo, for example, seedlings have been planted to replace trees cut out in routine control operations on the Old Station since 1940 and on the Square Mile since 1946, yet only a small proportion have been found with symptoms and cut out (Benstead, 1951, 1953). Similarly at the four WACRI Sub-stations in Ghana heavily infected farms have been cleared, replanted and brought back into bearing in areas of extensive infection. Less than 1 per cent. of the seedlings became infected in the six years after planting and most of the infections were on the perimeters of the plots, adjacent to infected trees on peasant farms.

These observations further emphasise the limited amount and extent of mealybug movement over any considerable distance. Clearly, in any future replanting in areas of swollen shoot infection the largest possible plots should be established and infected cacao trees and possible wild hosts removed from the plots and their perimeter. It is also possible that the likelihood of infection may be still further reduced by the use of resistant varieties, routine sprays, barrier crops or mild virus strains.

The Use of Resistant Varieties

Tests on seedlings and on rooted cuttings have shown that different

cacao types vary in susceptibility and in their reaction to infection (Posnette & Todd, 1951; Dale, 1957). Some Amazon material is difficult to infect and this suggests that resistant varieties may eventually provide a method of restricting virus spread. However, there is no information on the natural spread of virus in resistant material, although the laboratory tests are promising and indicate that some selections may show immunity in the field where they are not subjected to the heavy infestations of viruliferous mealybugs used in experiments. Some resistant types are also tolerant when infected and they may be particularly valuable in the field if these features are associated with low virus content and availability.

Mild Strain Protection

Some cacao viruses are able to protect plants from the effects of subsequent inoculation with more virulent strains, which suggests that young plants or trees around outbreaks of virulent virus could be protected by inoculating them with particularly mild forms (Posnette & Todd, 1955). These possibilities have recently been discussed (Thresh, 1958d) and the method may be valuable in certain heavily infected areas where eradication measures have been abandoned or are relatively unsuccessful. Nevertheless, further information is required on the performance of mild strains under field conditions, before they can be used on an extensive scale. In particular, information is required on the extent to which they check the spread of virulent strains and also on the rate at which mild strains spread into healthy cacao. Mild strains could only be used if they spread relatively slowly, otherwise they would cause a major problem, as they are difficult to detect.

SUGGESTIONS FOR FUTURE WORK

In each section of this bulletin, attention has been drawn to aspects of the work on swollen shoot disease on which information is lacking or inadequate. For convenience, the suggestions which have been made for further investigations are summarised in this section, although for practical reasons no attempt has been made to allocate an order of priority. However, observations which have been carried out to date on the spread of naturally occurring outbreaks in irregular cacao are of limited value and the most urgent need is for areas of regularly planted healthy cacao in which virus may be allowed to spread unchecked after being introduced according to a definite experimental design.

Mealybug Studies

Most of the observations on the distribution and behaviour of mealybugs on cacao have been on populations of *P. njalensis* on healthy trees at Tafo in Ghana. Nevertheless, information is still incomplete on the performance of this species as a vector of swollen shoot disease. Even less information is available on the mealybugs which are vectors of the disease in other countries. Further points requiring investigation include:

1. A survey of the composition of the mealybug populations on cacao in the different parts of the world where viruses occur.
2. The distribution of the various mealybugs on the different parts of infected trees.
3. The performance of the different mealybug species as vectors of the various cacao viruses.
4. The activity of the different stages of the various mealybug species and the relative frequency with which they are carried into the air by wind currents and move between trees.
5. The probability of mealybugs infecting healthy trees which they reach after walking through the canopy or by movement through the air for various distances.
6. The distance to which the various mealybugs are carried into the air and the gradients of their dispersal from a source.
7. The effect of seasonal factors on the size, composition, distribution and activity of the mealybug populations.
8. The incidence of mealybugs on young cacao and the effect of routine capsid control on the rate of build-up.
9. The effect of routine capsid control on the mealybug populations on sprayed trees.
10. The fate of mealybugs on trees which deteriorate in condition after becoming infected with virus.
11. The relation between ants and mealybugs.
12. An effective method of eliminating mealybugs on pods.

Virus Studies

Many aspects of the spread of virus require further investigation. These include a study of:

1. The factors influencing the availability of virus to mealybugs feeding on infected cacao trees and indigenous hosts of cacao viruses.
2. The incidence of natural infection in indigenous hosts and their importance as foci of infection in the various cacao areas.

3. The relationships between the viruses obtained from wild hosts and the viruses obtained from infected cacao in the same area.

4. The rate and pattern of spread from trees inoculated with viruses causing characteristic symptoms.

5. The rate of spread of virus in relation to tree population, age, condition and size of source.

6. The length of time which virus may remain latent in cacao material of different type and age.

7. The rate at which different viruses spread.

8. The rate at which virus spreads in material which tolerates or resists infection.

9. The incidence of virus in relation to the sites where pods are broken and the beans removed.

10. The number of mealybugs which remain on the pods at harvesting and are carried to the sites where the pods are broken and the beans removed.

11. The effect of insecticides on the rate of virus spread.

12. The effect of barrier crops and inter-cropping on the incidence and spread of virus.

SUMMARY

Cacao swollen shoot disease is spread by mealybugs which start new outbreaks by moving from the various sources of infection. Spread usually takes place within the crop, from trees (some of which were infected as clones) and from pods when these are harvested or distributed to provide seed. At least in West Africa indigenous trees are alternative sources of infection, from which virus may have spread into cacao. However they are now relatively unimportant in most localities, as virus is widespread and readily available in the introduced crop.

Observations on the uninterrupted spread of naturally occurring outbreaks in West Africa and Trinidad show that most new infections appear close to trees already showing symptoms and this is primarily due to the movement of immature mealybugs for short distances through the canopy. Immature mealybugs, particularly first instar nymphs, are also dispersed by wind currents and account for the relatively infrequent discontinuous spread over greater distances. Thus most new outbreaks are grouped around existing ones and their incidence decreases with increasing distance from them.

Rate of virus spread basically depends on the number of mealybugs moving from infected to healthy trees and this varies with seasonal and other factors affecting the size, composition, distribution and behaviour of the vector population. However, the proportion of active mealybugs which are viruliferous depends on the time spent on the infected host, the available virus and the rapidity with which they reach healthy trees. The proportion which actually transmit varies with the spacing, age and condition of the trees and on their susceptibility to infection.

Monthly observations on spread in Nigeria have shown a correlation between the annual number of new infections and the number of apparently healthy trees which were in contact with infected ones at the end of the previous year. Thus the annual number of new infections appearing around an outbreak tends to increase to a maximum and then declines as most of the trees become infected. Most of the infected trees in large outbreaks are not in contact with healthy ones and support relatively few mealybugs as they deteriorate in condition. By comparison the ratio of infected trees to healthy ones in contact with them is low around small outbreaks, which tend to spread at a relatively more rapid rate than large ones.

Cacao swollen shoot virus spreads slowly compared with other plant viruses and can be controlled by eradication measures, the efficiency of which depends upon the amount and extent of spread from latent and missed infections before these are eventually found and destroyed. The infected trees which are missed by the survey parties are relatively few around small outbreaks and occur over a limited distance compared with their distribution around large ones. Consequently small outbreaks are more readily controlled than large ones and cutting out treatments should vary with outbreak size. The present eradication measures may eventually be made more effective by using insecticides. These are now being applied to the apparently healthy trees around treated outbreaks in attempts to prevent spread from missed and latent infections until these are found and removed.

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APPENDIX I. THE SPREAD OF CACAO VIRUS ON THE EXPERIMENTAL AREA CRB. I. IN TRINIDAD. (DALE, 1953)

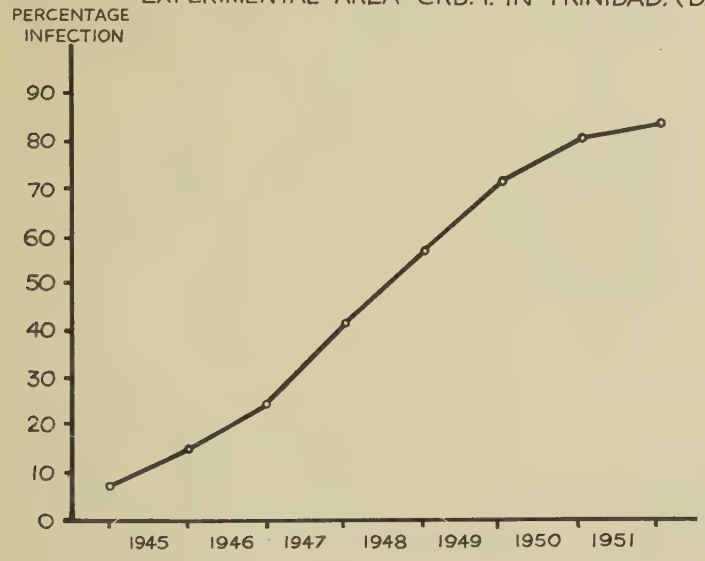


FIGURE 1. THE PERCENTAGE NUMBER OF TREES INFECTED EACH YEAR FROM 1944 TO 1951.

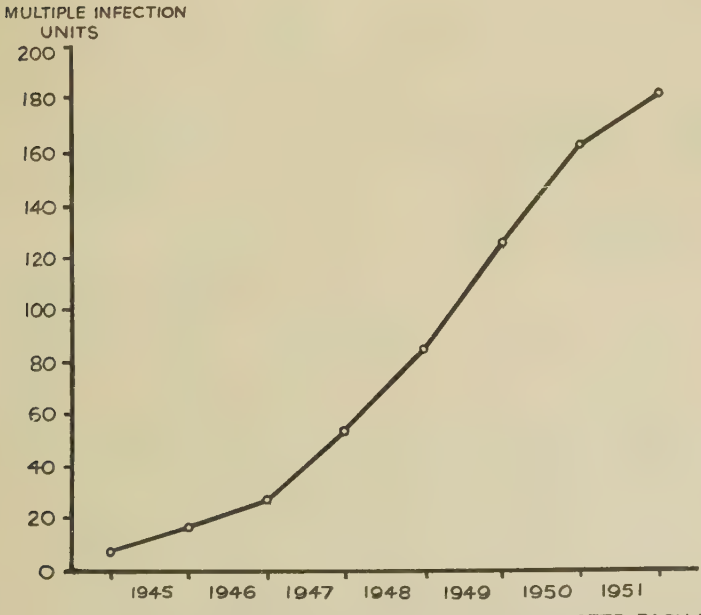
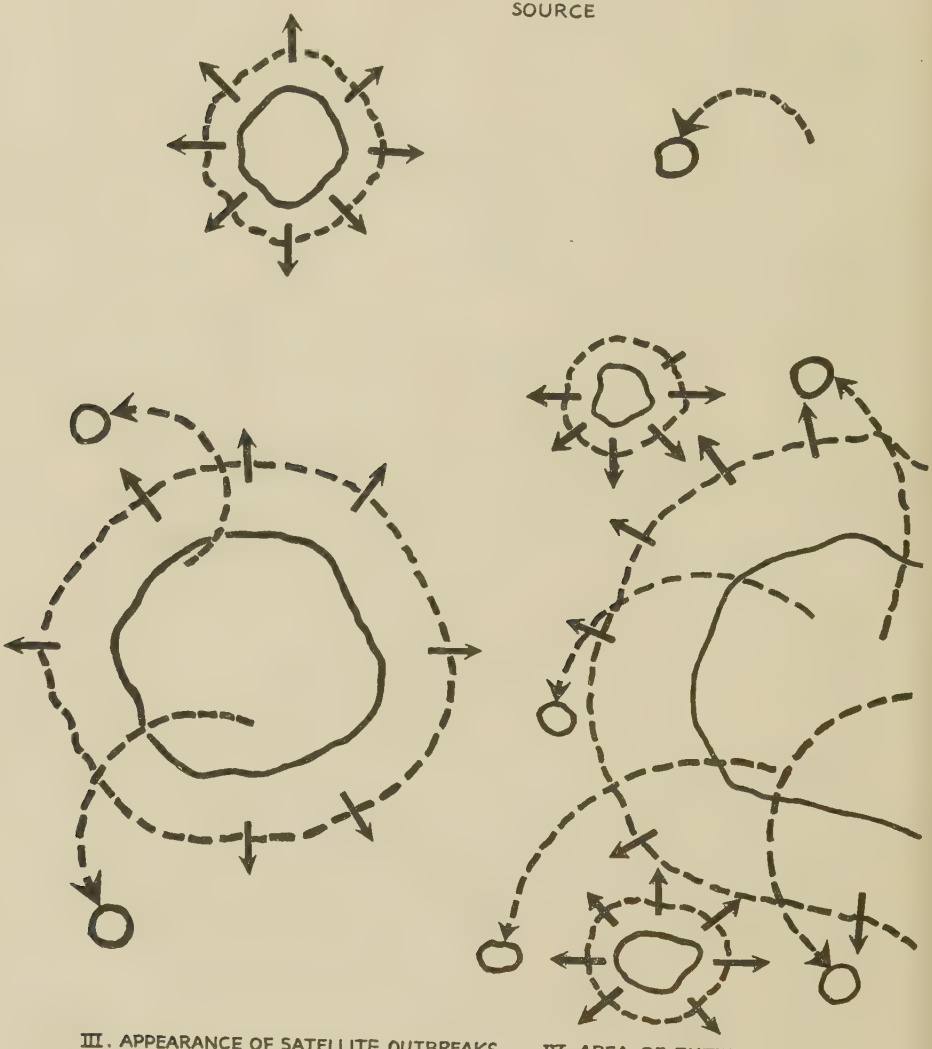


FIGURE 2. THE PERCENTAGE NUMBER OF TREES INFECTED EACH YEAR FROM 1944 TO 1951. DATA TRANSFORMED TO ALLOW FOR MULTIPLE INFECTION (GREGORY, 1948)

APPENDIX II. THE PATTERN OF SPREAD OF CACAO SWOLLEN SHOOT DISEASE



APPENDIX III

TABLE 1

Observations on the spread of cacao swollen shoot disease at Tafo, Ghana (Benstead, 1953)

Year	*Number of infected trees*	*Number of new infections*	*Percentage infection**	*Transformed percentages†*	*Rate of spread‡*
1945	1,450	—	31.3	37.5	—
1946	2,132	682	46.0	61.6	47.0
1947	2,967	835	64.0	102.2	39.2
1948	3,717	750	80.2	161.9	25.3
1949	4,144	427	89.4	224.5	11.5
1950	4,257	113	91.8	250.2	2.7
1951	4,270	13	92.1	253.9	0.3

* Based on the population of 4,636 trees present at the outset of the experiment.

† Percentages transformed by the multiple infection transformation of Gregory (1948).

‡ The number of new infections appearing each year as a percentage of the number of infected trees at the end of the previous year.

TABLE 2

Observations on the spread of cacao swollen shoot disease at Koroboto, Nigeria (Thresh, unpublished information)

Year	*Number of infected trees*	*Number of new infections*	*Percentage infection**	*Transformed percentages†*	*Rate of spread‡*
1953	59	—	7.1	7.4	—
1954	114	55	13.8	14.8	93.2
1955	194	80	23.5	26.8	70.2
1956	324	130	39.4	50.1	67.0
1957	456	132	55.1	80.1	40.7

* Based on the population of 827 trees present at the outset of the experiment.

† Percentages transformed by the multiple infection transformation of Gregory (1948).

‡ The number of new infections appearing each year as a percentage of the number of infected trees at the end of the previous year.

TABLE 3

Observations on the spread of swollen shoot disease on the Experimental Area CRB 1, Trinidad (Dale, 1953)

Year	*Number of infected trees*	*Number of new infections*	*Percentage infection**	*Transformed percentage†*	*Rate of spread‡*
1944	45	—	7.8	8.3	—
1945	91	46	15.8	17.4	102.2
1946	140	49	24.3	27.4	53.8
1947	242	102	42.0	54.5	72.9
1948	331	89	57.5	85.0	36.8
1949	412	81	71.5	125.0	24.5
1950	462	50	80.2	162.0	12.1
1951	482	20	83.7	181.0	4.3

* Based on the population of 576 trees present at the outset of the experiment.

† Percentage transformed by the multiple infection transformation of Gregory (1948).

‡ The number of new infections appearing each year as a percentage of the number present at the end of the previous year.

TABLE 4

Observations on the spread of cacao swollen shoot disease in naturally occurring outbreaks at Amafie and Bosumuoso in the Western Province of Ghana (Posnette & Todd, unpublished information)

Year	*Amafie*			*Bosumuoso*		
	Number of infected trees	*Percentage infection**	*Rate of spread†*	*Number of infected trees*	*Percentage infection**	*Rate of spread†*
1946	158	9.5	—	29	2.5	—
1947	243	14.6	55.1	118	10.4	306.9
1948	399	24.0	64.2	358	31.4	203.4
1949	530	31.9	32.8	606	53.2	69.3
1950	591	35.6	11.5	665	58.4	9.7
1950‡	678	40.8	—	760	66.7	—

* Based on the population of 1,661 trees originally present at Amafie and 1,139 at Bosumuoso.

† The number of new infection appearing each year as a percentage of the number of infected trees at the end of the previous year.

‡ All the trees were coppiced at the conclusion of the experiment and in this way many latent infections were discovered.